# Assessing the abundance of seven major arthropod groups along an altitudinal gradient and across seasons in subtropical rainforest

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## ABSTRACT

Changes in the abundance of seven major arthropod taxa with changes in altitude and season were investigated in a subtropical rainforest using both Malaise traps and flight intercept traps. Sampling was conducted as part of the IBISCA-Queensland Project at four plots established at each of five altitudes (300, 500, 700, 900 and 1100 m above sea level) within continuous rainforest. Trapping was carried out at four times throughout a 12 month period, comprising a dry season (winter) sample and samples in the early (spring), mid (summer) and late (autumn) wet season. Clear seasonal changes in the abundance of arthropods sampled were evident as well as changes in community assemblages. The winter sample in particular was different to all other seasons. Limited response to altitude was detected, with the greatest differences between altitudes along the gradient found in summer and winter samples. The limited altitudinal trend is likely the result of the scale of sampling with individual species and families expected to show contrasting responses. The clear influence of season, however, does demonstrate the sensitivity of these broad arthropod groups to climate variability and cues. ☐ *IBISCA, arthropod, subtropical rainforests*.

Changes in environmental conditions associated with changes in altitude are well known and broadly predictable. As altitude increases, temperature and partial pressure of atmospheric gases will decrease; rainfall, UV radiation and wind speed can be expected to increase. The abundance and diversity of different arthropod groups might, as a result of these environmental changes, be expected to change with increasing altitude, although responses are likely to vary among different taxa. For example, some groups or species may be widely distributed along an altitudinal gradient, while others might specialise in particular extremes of the climate continuum associated with changes in altitude. These distributions of individual organisms may be related to differences in life history, behaviour or interactions with other organisms associated with changes in environmental conditions (Hodkinson 2005) as is the case along other environmental gradients.

Given that temperature (Chen *et al.* 2009) and moisture are considered important influences

on arthropod life histories, arthropods, and in particular insects, would be expected to respond to environmental changes associated with changes in altitude. A simple correlation between known environmental conditions and the physiology, behaviour and life history of major arthropod groups might suggest *a priori* predictions of dominance of particular arthropod groups under different microclimatic conditions. For example, flies require moist conditions for larval development and this would suggest larger populations in moist environments. By contrast, for ants ground nesting is difficult under wet conditions and arboreal nesting is limited by cold conditions, so they would not be expected to be very successful in the cool wet conditions of mountain tops (Janzen 1973). Some general trends in pollinator dominance in relation to altitude have been identified in temperate systems. A decreasing number of plants are pollinated by Hymenoptera with increasing altitude, whereas Lepidoptera and in particular Diptera, become increasingly important pollinators along the same gradients (Arroyo *et al.* 1982; Warren *et al.* 1988). In these temperate systems, two explanations for these trends have been proposed. First, a reliance on endothermically generated energy in Hymenoptera, versus lengthy sun basking in the other two orders, may place them at a competitive disadvantage in higher, colder altitudes (Arroyo *et al.* 1982; Warren *et al.* 1988). In contrast, differences in flower morphology between high and low elevations was considered by Warren *et al.* (1988) to present a competitive advantage to Hymenoptera at lower elevations. This second hypothesis suggests that elevational patterns might be driven by competition among pollinators for flowers, rather than by competition between plant species for pollinators, as implied by the insect thermoregulatory basis of the former hypothesis. However, Warren *et al.* (1988) concluded that the dominance of flies at high altitudes (70% of the flora was pollinated by flies) was the result of insect physiology. By contrast, in reviewing the changing abundance of herbivorous insects with altitude, Hodkinson (2005) demonstrated that

populations of individual species of flies, beetles and moths showed both increases and decreases with increasing altitude. His conclusion was that any a priori simple correlation with climatic change would be masked by complex interactions with other species of both plants and animals.

Lamington National Park in southeast Queensland, presents an opportunity to consider patterns of insect diversity along an altitudinal gradient. Lamington National Park supports extensive areas of subtropical rainforest (see Laidlaw *et al.* 2011 for a review of the rainforest types represented in the park) and encompasses altitudes ranging from approximately 250 m a.s.l. to close to 1200 m a.s.l. The IBISCA-Queensland Project (see Kitching *et al.* 2011) set out to determine the distribution of arthropod groups along an altitudinal gradient using multiple sampling methods. An altitudinal gradsect was established in Lamington National Park with four plots at each of five altitude categories (300, 500, 700, 900 and 1100 m a.s.l.) giving a total of 20 plots. Using these plots, a "baseline" arthropod survey was conducted in which a standard set of traps were deployed. Most of the baseline sampling methods were repeated in each of four seasons across a 12 month period. Details of the trapping program are provided in Kitching *et al.* (2011). Here we focus on two trapping methods – Malaise traps and flight intercept traps (FITs). Both methods capture a high number and diversity of flying insects, but Malaise traps are particularly effective at collecting Diptera and Hymenoptera (Campbell & Hanula 2007) while Coleoptera are particularly well sampled by flight intercept traps (Southwood & Henderson 2000).

Using the abundances of seven major arthropod groups collected over four seasons in both Malaise and flight intercept traps (FITs) we initially tested whether the overall abundance of different arthropod groups changed between seasons. We expected considerable differences in overall abundances between samples collected in the cool, dry winter (July) and those collected in other seasons. However, differences between

samples collected during the transition from the dry season to the wet season (October), the mid-wet season (January) and the end of the wet season (March) are less predictable. Our second aim was to determine if the overall abundance of different arthropod groups changed with increasing altitude. In particular, are there changes in the dominant arthropod groups from low to high altitudes? For example, we might expect an increase in Diptera and corresponding decrease in Hymenoptera at progressively higher altitudes. We then tested whether altitudinal patterns were consistent across all four sampled seasons. We also discuss the similarities and differences between the results of the two different trapping methods.

## MATERIAL AND METHODS

**Study site.** Sampling was conducted at each of four IBISCA-Queensland plots established within five altitudinal zones (300, 500, 700, 900 and 1100 m a.s.l.) along an altitudinal gradsect in Lamington National Park as described in detail by Kitching et al. (2011). All plots were located on basalt derived soils with rainforest the broad vegetation type (Laidlaw et al. 2011). The area is characterised by summer dominant rainfall, with summer falls (on average 200 mm) reaching a peak in January. A comprehensive discussion of micrometeorological conditions of the plots can be found in Strong et al. (2011).

**Trapping.** Single Malaise and flight intercept traps (FITs) were placed within fifty metres of the post located in the centre of the 20 x 20 m quadrat of each of the twenty IBISCA-Queensland plots (see Kitching et al. 2011). In this way four trap replicates were obtained at each of five altitudes. The Malaise trapping program was described in detail in Lambkin et al. (2011). Each FIT consisted of a vertical rectangular panel (66 x 70 cm) of layers of transparent plastic kitchen film, wrapped around two wooden posts, above a rectangular collecting container (14 x 66 cm) raised above ground level and filled with propylene glycol. A roof was erected over the trap array to prevent water inundating the collection containers. Traps were operated for 10 days at each plot. Both Malaise and FIT traps were set and operated four times over the course of a twelve month period; October 2006, January 2007, March 2007 and July 2007. Samples were stored in 70% ethanol and returned to the laboratory for sorting. Individuals from all major arthropod groups were sorted and counted. Arthropod groups selected for analyses were Thysanoptera, Heteroptera, Diptera, Coleoptera, Hymenoptera and Araneae. In addition, Hymenoptera were subdivided into ants (family Formicidae) and all other Hymenoptera as this was easily achieved and we strongly suspected ants would respond to altitude. These groups are megadiverse arthropod taxa and those for which taxonomic expertise was available for further identification as part of the broader IBISCA-Queensland program. This paper reports only these seven taxa selected for further study.

**Analysis.** To determine if assemblages of the seven major arthropod taxa changed with altitude and if these trends were consistent among seasons, we used non-parametric multivariate two-way analysis of variance (NPMANOVA, Anderson 2001) using PRIMER 6 and PERMANOVA+ software packages (Clarke & Gorley 2006; Anderson et al. 2009). This approach makes no assumptions about underlying data distributions and generates a pseudo $F$-value analogous to the familiar parametric $F$ of Fisher with probability values calculated by permutation (Anderson 2001). Separate analyses were conducted for Malaise and FIT samples, based on Bray-Curtis dissimilarity index values, using abundance data (log-transformed and then standardised by sample size), with 4999 permutations. Although this is a multivariate analysis analogous to repeated measures ANOVA, no correlation structures through time (sphericity) were assumed as sampling events were separated by an adequate amount of time (at least three months) (Anderson et al. 2009).

NPMANOVA was also used to make post-hoc pair-wise comparisons. Due to the small number of replicated samples per treatment, the number of unique permutations was limited for each pair-wise comparison. Consequently, Monte Carlo asymptotic permutation was conducted to calculate $P$ values. Because of the number of pair-wise comparisons the chances of a Type I error increased and this should be taken into account when determining the significance of probability values (for example by applying a Bonferroni correction). Significant levels were, however, not changed as the minimum $P$ value for 4999 permutations ($P$=0.002) was greater than Bonferroni corrected $P$ values (e.g. $P$=0.001 for 40 pair-wise comparisons).

Non-metric multi-dimensional scaling (NMDS) was then used to create ordination plots for both the Malaise and FIT datasets to visually explore the results of the NPMANOVA. These ordinations were calculated using the software package PRIMER 6 (Clarke 1993; Clarke & Gorely 2006) using 25 restarts.

TABLE 1. Results of non-parametric multivariate analyses of variance carried out on the abundance of seven arthropod groups along an altitudinal gradient at four times of the year (seasons) using two insect trapping methods , Malaise traps and flight intercept traps (FITs).

|  |  | df | F | $P$ (perm) |
|---|---|---|---|---|
| Malaise Traps | Season | 3 | 32.4265 | 0.0002 |
|  | Altitude | 4 | 3.8535 | 0.0002 |
|  | Season × Altitude | 12 | 1.89791 | 0.0126 |
| FITs | Season | 3 | 34.3645 | 0.0002 |
|  | Altitude | 4 | 6.7559 | 0.0002 |
|  | Season × Altitude | 12 | 1.7985 | 0.0472 |

TABLE 2. Summary results of post-hoc tests comparing differences in ordinal assemblages between pairs of seasons using Malaise traps and FITs. Due to a significant interaction between altitude and season, separate post-hoc tests were executed for each of the five altitudinal zones. $P$ values were calculated by 4999 Monte Carlo asymptotic permutations. Significant $P$ values are shown in bold.

| Trap Method | Groups | $P$ (MC) values | | | | |
|---|---|---|---|---|---|---|
|  |  | 300 m | 500 m | 700 m | 900 m | 1100 m |
| Malaise | Oct, Jan | 0.084 | 0.256 | 0.123 | 0.091 | 0.103 |
|  | Oct, Mar | 0.185 | 0.585 | 0.568 | 0.009 | 0.264 |
|  | Oct, Jul | 0.035 | 0.008 | 0.016 | 0.015 | 0.003 |
|  | Jan, Mar | 0.708 | 0.369 | 0.356 | 0.046 | 0.106 |
|  | Jan, Jul | 0.019 | 0.008 | 0.008 | 0.081 | 0.002 |
|  | Mar, Jul | 0.044 | 0.007 | 0.027 | 0.035 | 0.003 |
| FITs | Oct, Jan | 0.437 | 0.105 | 0.096 | 0.131 | 0.029 |
|  | Oct, Mar | 0.160 | 0.086 | 0.019 | 0.018 | 0.004 |
|  | Oct, Jul | 0.006 | 0.005 | 0.008 | 0.008 | 0.006 |
|  | Jan, Mar | 0.239 | 0.821 | 0.043 | 0.055 | 0.001 |
|  | Jan, Jul | 0.002 | 0.019 | 0.006 | 0.006 | 0.002 |
|  | Mar, Jul | 0.005 | 0.088 | 0.022 | 0.015 | 0.002 |

TABLE 3. Summary results of post-hoc tests comparing differences in ordinal assemblages between pairs of altitudes collected in Malaise traps and FITs. Due to a significant interaction between altitude and season, separate post-hoc tests were executed for each of the four seasons. $P$ values were calculated by 4999 Monte Carlo (MC) asymptotic permutations. Significant $P$ values are shown in bold.

| Trap Method | Groups | $P$ (MC) values | | | |
|---|---|---|---|---|---|
| | | October (spring) | January (summer) | March (autumn) | July (winter) |
| Malaise | 300m, 500m | 0.550 | **0.015** | 0.375 | 0.197 |
| | 300m, 700m | 0.702 | 0.068 | 0.401 | 0.400 |
| | 300m, 900m | 0.260 | **0.011** | **0.044** | 0.767 |
| | 300m, 1100m | 0.425 | **0.001** | 0.126 | **0.046** |
| | 500m, 700m | 0.753 | 0.148 | 0.776 | 0.189 |
| | 500m, 900m | 0.623 | 0.068 | **0.037** | 0.135 |
| | 500m, 1100m | 0.201 | **0.008** | 0.234 | **0.030** |
| | 700m, 900m | 0.377 | 0.122 | 0.282 | 0.712 |
| | 700m, 1100m | 0.163 | **0.026** | 0.186 | **0.006** |
| | 900m, 1100m | 0.861 | 0.139 | 0.061 | **0.019** |
| FITs | 300m, 500m | 0.484 | 0.644 | 0.752 | 0.309 |
| | 300m, 700m | 0.180 | 0.396 | 0.174 | 0.141 |
| | 300m, 900m | 0.307 | 0.114 | 0.077 | **0.049** |
| | 300m, 1100m | 0.063 | **0.005** | **0.047** | **0.009** |
| | 500m, 700m | 0.123 | 0.277 | 0.336 | 0.807 |
| | 500m, 900m | 0.575 | 0.356 | 0.247 | 0.760 |
| | 500m, 1100m | 0.107 | **0.006** | 0.334 | 0.245 |
| | 700m, 900m | 0.269 | 0.162 | 0.506 | 0.303 |
| | 700m, 1100m | **0.043** | **0.002** | 0.079 | 0.127 |
| | 900m, 1100m | 0.183 | **0.007** | 0.439 | 0.570 |

## RESULTS

The total number of individuals collected in each sample was highly variable. Malaise traps collected many more individuals (n = 187504) than did the FITs (n = 33487). There was, as expected, considerable seasonal variability with substantially less insects collected in the dry, cooler season (July 2007) compared to all other seasons. This was the case for both Malaise traps (July total = 25754) and FITs (July total = 4060).

Total trap catches in July were less than half those in March (Malaise = 63385 and FITs = 8302) and January (Malaise = 63313 and FITs = 10887). In the case of the FITs, the October catch (12480) was almost three times the July catch. However, although higher than the July catch, the Malaise catch for October (37808) did not display the same large increase seen in the FITs. Diptera dominated (85% of the catch) the Malaise trap catches in all seasons and at all altitudes. While Diptera were a strong faunal element in the FIT catches (30%),
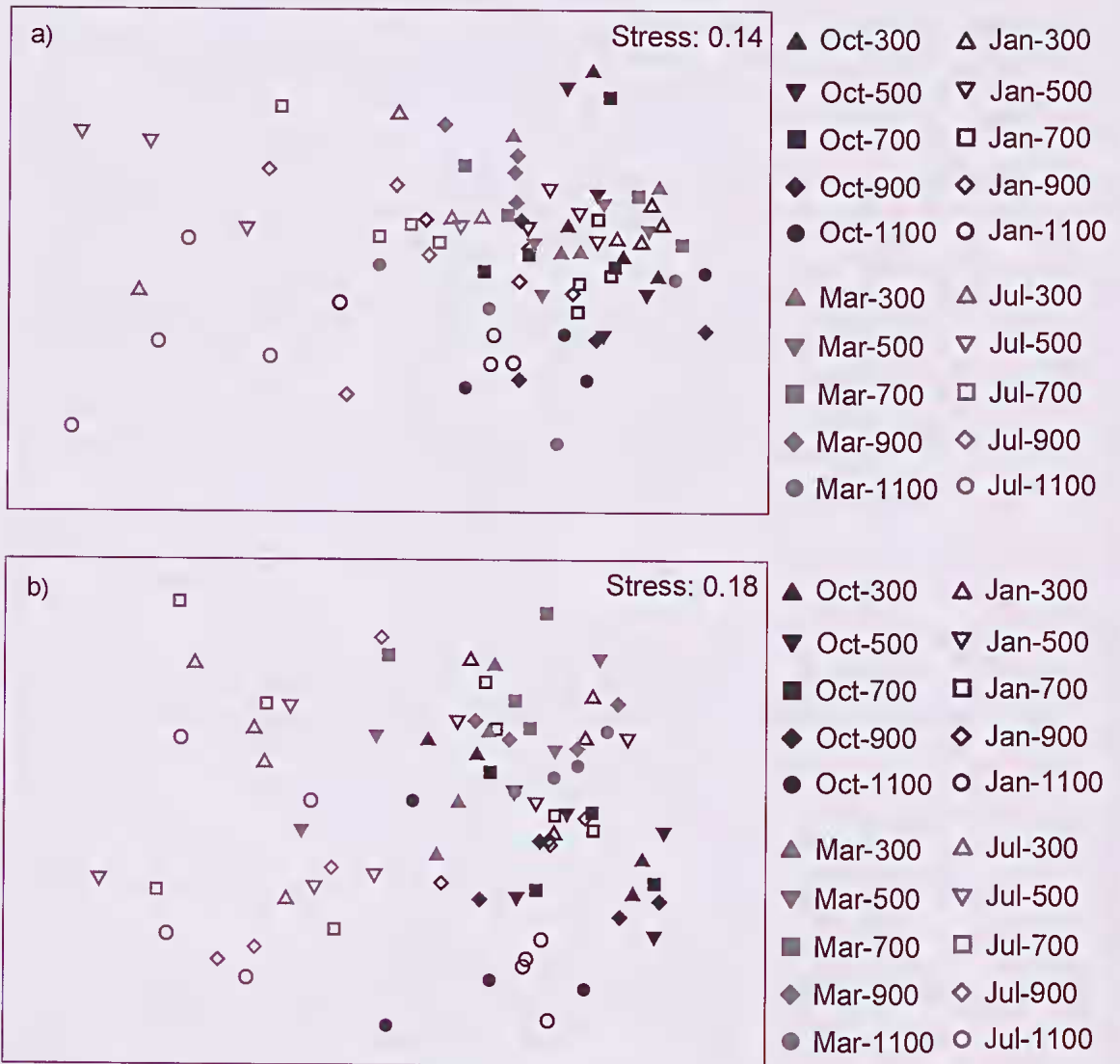
FIG. 1. Ordination plot based on a multi-dimensional scaling analysis of the relative abundance of seven arthropod taxa caught across five altitudinal zones (four plots in each of 300, 500, 700, 900 and 1000 m a.s.l.) in each of four seasons using (a) Malaise traps and (b) flight intercept traps.

Coleoptera were the most abundant group (54%) in these traps at all altitudes and in all seasons with the exception of July when Diptera were more abundant at all altitudes.

**Altitude and Season.** We first investigated the effects of altitude and season on the assemblage composition of the target arthropod groups. Although the results of NPMANOVA showed
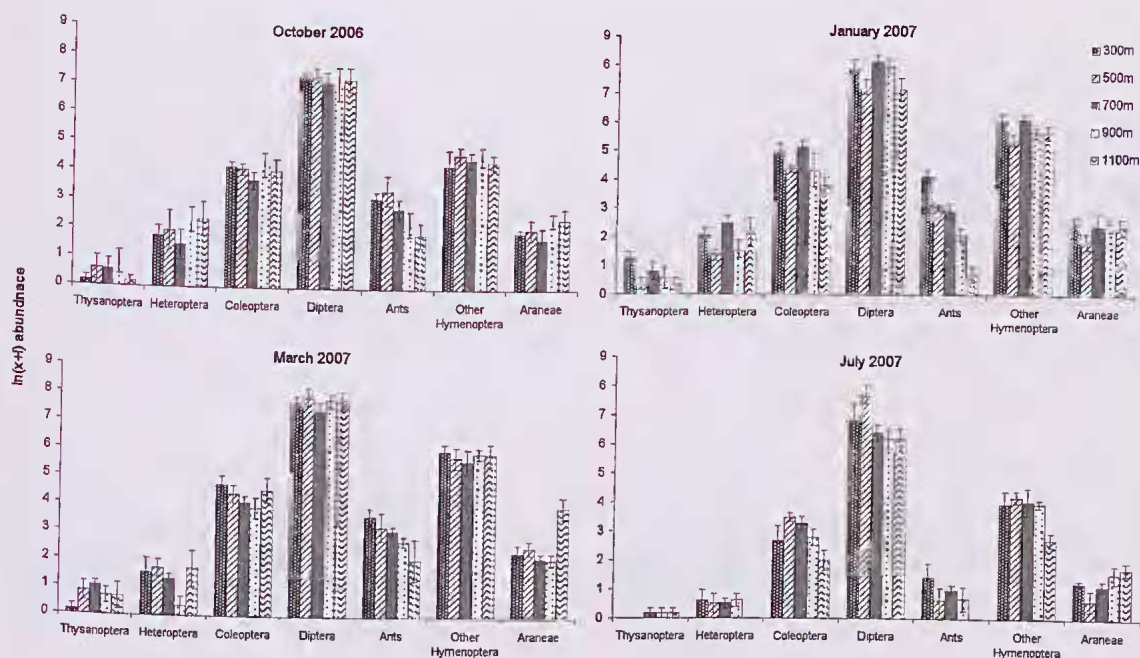
FIG. 2. Natural log-transformed (x+1) mean abundance (± S.E.) of arthropod groups caught by Malaise traps at four plots within each of five different altitudes (m a.s.l.) in four seasons; spring (October 2006), summer (January 2007), autumn (March 2007) and winter (July 2007).

significant effects of both season and altitude, their interaction effect was also significant for both trap methods (Table 1). This suggests that the differences between altitudes were expressed differently between seasons (and vice versa). Consequently post-hoc analyses were restricted to the investigation of arthropod assemblages between seasons within each of the five altitudes (Table 2), and investigation of arthropod assemblages between altitudes within each of the four seasons (Table 3).

The NPMANOVA procedure provides the capacity to test *a posteriori* pair-wise combinations of the interaction terms and when this was done for the interaction of season and altitude on the seven arthropod groups collected by Malaise traps, a number of pair-wise comparisons demonstrated a significant difference at $P < 0.05$ (Tables 2 and 3).

Looking first at changes in assemblages between seasons at individual altitudes, significant differences between at least two seasonal assemblages were experienced at all altitudes, with assemblages collected by FITs from 1100 m a.s.l. significantly different between all seasons (Table 2). Most frequently, winter samples (July) were significantly different to those from all other seasons (Table 2). When we consider changes in assemblages across altitude within each individual season, fewer significant pairwise comparisons are apparent (Table 3). Most altitudinal change in assemblages was confined to winter (July) and summer (January) (Table 3), with only one significant difference (700 m v 1100 m FIT) demonstrated in spring (October). The assemblages of highest and lowest altitudes were more likely to be significantly different compared to those from adjacent altitudes (Table 3).
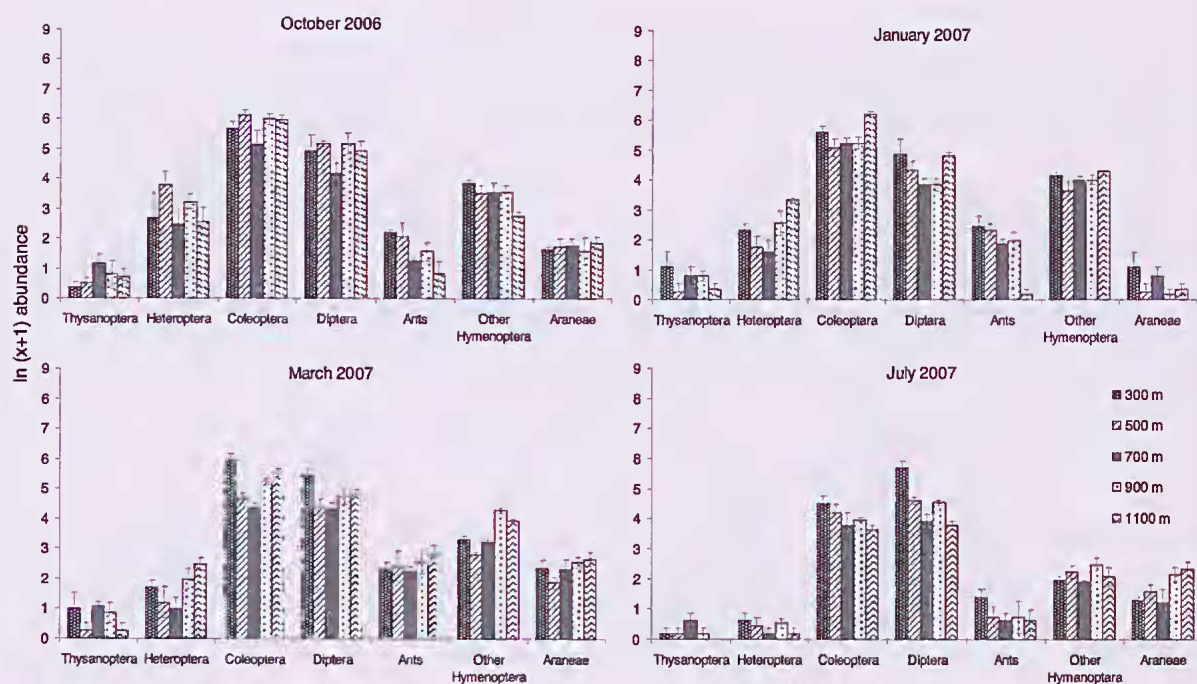
FIG. 3. Natural log-transformed (x+1) mean abundance (± S.E.) of arthropod groups caught by flight intercept traps at four plots within each of five different altitudes (m a.s.l.) in four seasons; spring (October 2006), summer (January 2007), autumn (March 2007) and winter (July 2007).

The complicated nature of the interaction of season and altitude on assemblages of the target taxa is apparent from the NMDS ordinations. The influence of season is somewhat easier to visualise, with winter samples (from both collecting methods) clearly separated from those of other seasons, but there is no clear altitudinal pattern of assemblages (Fig. 1).

When looking at the abundance data for individual taxa, there was no consistent altitudinal trend for all groups in all seasons (Figs 2 and 3). The abundances of some taxa appeared relatively constant across all altitudes, while for other taxa there did not appear to be a simple linear relationship between abundance and altitude. The Diptera are a case in point, with most seasons showing no clear pattern between abundance and altitude except for the July FITs samples where there was a steep decline in dipteran abundance

with increasing altitude (Fig. 3). Ants showed the clearest altitudinal response, a linear-decline in abundance with increasing altitude, and this trend was consistent across most seasons and both trapping methods. Spiders either showed similar abundances across all altitudes or increased in abundance with increased altitude, with the clearest trend observed in July (Fig. 3).

## DISCUSSION

Our results demonstrate that the abundance and community dominance of major arthropod taxa in response to increasing altitude is complex. The expectation that some groups would decline steadily with altitude, while others increased, was simply not the case (with the exception of ants). The total abundance of individuals did change from season to season, as was expected, with the

Malaise traps in particular collecting dramatically greater numbers of the focal taxa in the wet season months of January and March, indicating that most flight activity occurs during this time. The very low abundances recorded from both trapping methods in the drier and cooler winter season (July sample) is consistent with other seasonal surveys of tropical insect abundance (e.g. Frith & Frith 1985; Wilson *et al.* 2007).

The abundances of some of the focal arthropod groups changed consistently with respect to altitude, however, the patterns were not consistent across all seasons. In this study, season appeared to have the strongest influence on the abundances of the focal groups rather than altitude. However, this does not mean that altitude is unlikely to influence the abundance and dominance of some groups, but rather that the relationship between abundance and altitude is under a strong seasonal influence.

Strong seasonal differences were detected within altitudes, particularly between winter (July) samples and those of all other seasons. This was particularly the case for all altitudes and both trapping methods when assemblages from October and July were compared. Winter samples (July) were generally characterised by low total abundances at all altitudes, with substantially lower catches at 700 m a.s.l. and above. This contrasted to the situation in the wetter, warmer months (October, January and March) in which the total trap catches were lowest at either the 500 or 700 m a.s.l. plots. This pattern was apparent for all the mega-abundant groups, *viz.* Diptera, Coleoptera and Hymenoptera (excluding ants).

Significant differences in the assemblage composition of the focal taxa between different altitudes were detected, although almost exclusively in summer (January) and winter (July). This again emphasises the importance of season in determining the assemblage of arthropod groups at a given altitude. Hodkinson (2005), in a review of a number of altitudinal population studies of insects, concluded that there was no consistent

response in abundance within Orders with both altitudinal increasers and decreasers found. Our study considers arthropods at a very coarse taxonomic scale, and the weak altitudinal patterns we observed are likely a reflection of the unique and inconsistent responses of the individual species within each order to altitude and therefore micro-climatic conditions. Our study does, however, emphasise the role of season in accentuating altitudinal responses. We know that insects at the extremes of their altitudinal range can have very different morphologies, behaviours and life history patterns (Hodkinson 2005). As the seasons and their climatic conditions shift, so too might the populations of species at the extremes of their ranges. Seasonal shifts in species have demonstrated the link between microclimatic conditions and shifting species distributions (Menéndez & Gutiérrez 2004).

In our study, abundances of Hymenoptera (excluding ants) did not display a consistent altitudinal trend, with just the October FIT and July Malaise samples showing an apparent decrease in abundance with increasing altitude. This contrasts with consistent declines in the importance of hymenopteran pollinators with increasing altitude found in temperate regions. Consequently we found no evidence of an endothermic disadvantage to Hymenoptera at cool, high altitudes (Arroyo *et al.* 1982; Warren *et al.* 1988).

## CONCLUSIONS

The general intent of this study was to determine if the abundances and composition of major arthropod groups change with altitude and if such changes are consistent across seasons. The significant results of testing season, altitude and the interaction of these factors using the non-parametric MANOVA demonstrate that differences between altitudes in each season were not random. However it is difficult to determine a clear and consistent trend. The sampling effort at each altitude was restricted to four samples. The

highly variable catches in each trap suggest that greater numbers of replicates might give a clearer picture, although sorting more samples would be problematic. It is also important to bear in mind that this study looked only at one 12 month period. No doubt repeated ongoing surveys would help clarify patterns.

## ACKNOWLEDGEMENTS

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